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## The water-storing tubers of plants

JOHN W. HARSHBERGER

(WITH PLATE 17)

Recently there has been brought to the attention of the writer a number of plants that produce water-storing organs of an interesting morphologic character. They were examined in the fresh condition in free-hand sections and a number of microchemic tests were applied in order to ascertain the character of the respective reserve materials. Two species of ferns, *Nephrolepis cordifolia* from the garden of Dr. P. P. Calvert and *Nephrolepis davallioides* Kze. [*N. acuminata* (Houtt.) Kuhn] from the fernery of Mr. John P. Morris, of Chestnut Hill, were examined in detail. *Asparagus Sprengeri*, a much cultivated species of asparagus, was also studied.

*Nephrolepis cordifolia* (L.) Presl. [*N. tuberosa* (Bory) Willd.] is a fern which is often found in cultivation. It is easily mistaken for the sword-fern, *N. exaltata*, but it differs from that fern in having shorter fronds and the pinnules more closely crowded together. It resembles *N. philippinensis* Hort.,\* also found frequently in cultivation. *Nephrolepis cordifolia* is said to occur in northern India, Japan, Australia, New Zealand, tropical east and west Africa and in the whole of tropical America, growing on the ground, as well as epiphytic on trees. It has short, thick rhizomes covered by broken-off leaf-bases and numerous strong branches are formed, some of which are developed in midsummer as fleshy tubers which are about the size of pigeon-eggs (PLATE 17, FIGURE 1). More exactly, a mature tuber measured by me was in three dimensions, twelve millimeters, twenty-eight millimeters, and three millimeters. Christ† states that these tubers store reserve products of use to the plant in its epiphytic existence. Mrs. J. M. Milligan‡ of Jacksonville, Florida, found tubers on a specimen of

\* BAILEY, in the Cyclopaedia of American Horticulture, gives this (*N. philippinensis*) as probably belonging to *N. exaltata*.

† CHRIST. Die Farnkräuter der Erde, 288.

‡ MILLIGAN, Mrs. J. M. Tubers of *Nephrolepis*. Fern Bulletin 7 : 12. 1899.

*Nephrolepis*, called by her *N. exaltata*, while changing the fern from one pot to another. The tubers, she says, were of all sizes up to three fourths of an inch in diameter and irregularly rounded. No indications of buds were discovered and some of the largest tubers were planted, but did not grow.

In all probability, as pointed out by J. Birkenhead,\* the fern described by Mrs. Milligan as *N. exaltata* was *N. cordifolia* (= *N. tuberosa*). *Nephrolepis philippinensis* produces tubers in profusion, so also do *N. Pluma* var. *Bausei* and *N. undulata*, all deciduous ferns. A peculiar feature of these deciduous ferns, Birkenhead states, is that the plant of one season does not always grow again from the old caudex, but there is in many cases a tuber formed close to the old caudex, from which growth commences in due course the following season. The other tubers formed at various distances away from the main stem also commence growth and produce plants. One of the points which distinguish *N. pectinata* from the others, as Clute adds editorially in commenting on Birkenhead's article, is the absence of tubers. *Adiantum diaphanum* (*A. setulosum*) produces tiny tubers on its roots, the size of mustard seeds, some roots bearing twenty to thirty tubers in a length of three to four inches. Velenovsky † in his *Vergleichende Morphologie der Pflanzen* also describes the tubers of *Nephrolepis cordifolia* (= *N. tuberosa*).

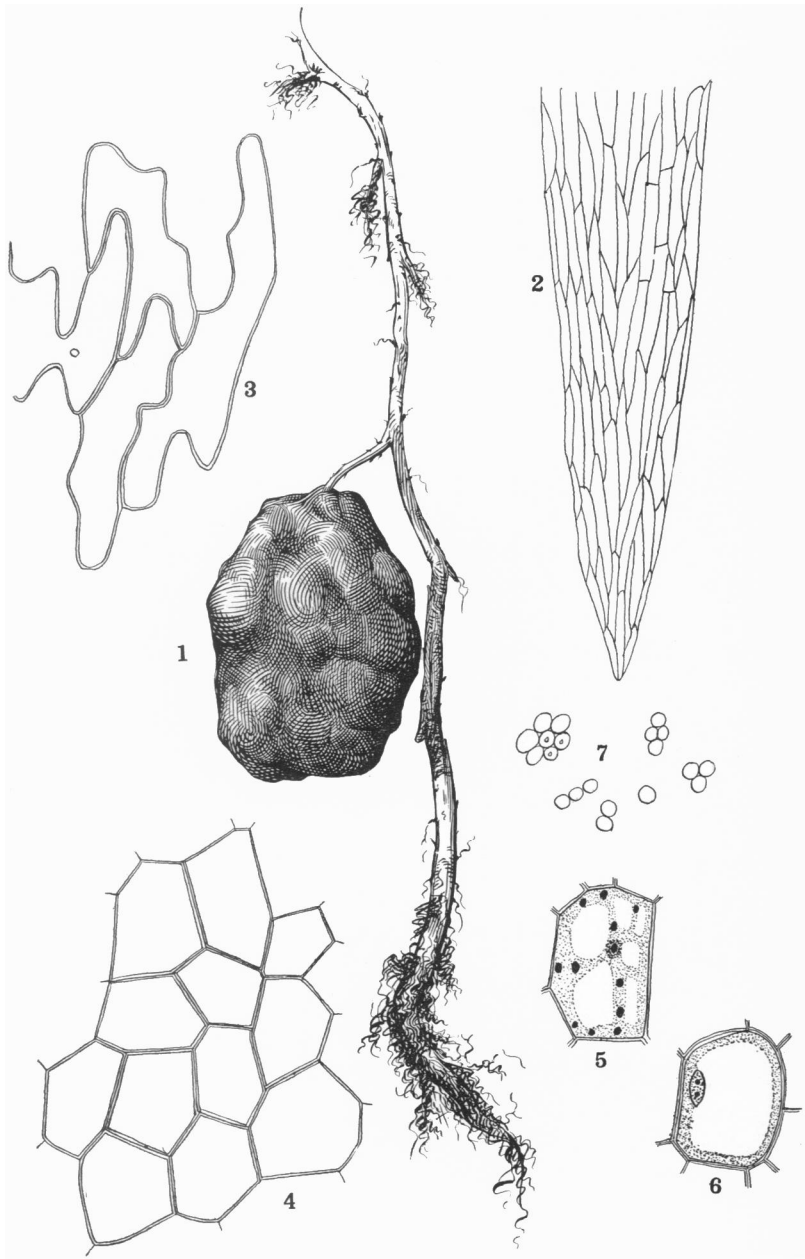
Le Maout and Decaisne mention *Nephrodium esculentum* ‡ of Nepaul that furnishes edible tubers used by the natives. Heinricher, § in a paper published since the above statements were written by me, has presented a complete study of the regeneration of several species of *Nephrolepis* from the fleshy tubers noticed above, when these are cut and experimentally treated. He finds that tubers are formed on *N. cordifolia* Presl (= *N. tuberosa* Presl), *N. hirsutula* (Forst.) Presl, *N. Pluma* Moore, and *N. philippinensis* Hort. He distinguishes two forms of *N. cordifolia*, viz., subspecies

\* BIRKENHEAD, J. Tubers of *Nephrolepis*. Fern Bulletin 7 : 35. 1899.

† VELENOVSKY, J. *Vergleichende Morphologie der Pflanzen*, Teil I. Prag, 1905.

‡ I cannot find this name, but give it as a quotation.

§ HEINRICHER, E. Zur Kenntnis der Farngattung *Nephrolepis*. Flora 97 : 43-73. pl. 1, 2. 28 D 1906. *N. Pluma* Moore is considered a variety of *N. cordifolia*.



WATER-STORING TUBERS

(a) *tuberosa* and subspecies (b) *etuberosa*. The regeneration from tubers in *N. cordifolia* subsp. *tuberosa*, in *N. hirsutula*, in *N. Pluma*, and in *N. philippinensis* consists in the formation of stolons with a central axial bundle system and normal green pinnae arising from these ramentae-covered stolon-like branches. His photographic illustrations show the character of the various forms of tubers in a very satisfactory manner. Incidentally, Heinricher states that in *N. cordifolia* the tubers serve for the storage of water. In the large parenchyma-cells of the tubers of *N. hirsutula* Heinricher found small starch grains (?), which in no case completely filled the cells, and such cells reacted to Fehling's solution, indicating the presence of sugar. Sperlich likewise claims that he found the cells of young tubers filled with starch, while in the mature tubers the starch grains were sparingly found, but the sugar content had increased proportionately.

My observations on the structure of fern tubers, now to be recorded, are at variance with the above statements in the two species of *Nephrolepis* investigated by me, viz., *N. cordifolia* and *N. davalloides*. In these two ferns, the lateral cord-like branches with small hair-like ramentae are brown in color (PLATE 17, FIGURE 2). These ramentae extend also to the wrinkled surface of the tuber, but are more sparingly found. A microscopic examination of the tuber surface shows that it consists of large epidermal cells, the walls of which interlock by sinuous lines (PLATE 17, FIGURE 3). The interior of the tuber is found to consist of large, rounded hexagonal, or pentagonal parenchyma-cells, with thin walls (FIGURE 4), while the fibrovascular elements are arched near the surface, running from base to apex. These parenchymatous cells in the freshly cut tubers are filled with watery protoplasm, and the observer is impressed by the absence of solid reserve food. Considerable protoplasm with a large nucleus is present in the younger cells (FIGURE 5), but in the older cells the protoplasm and nucleus are confined to a thin wall-layer, as the sap vacuole increases in size (FIGURE 6). Treatment with iodine fails to reveal the presence of starch and protein. Water-eosin colors the protoplasm but slightly, and this reaction, as also the application of Bismarck brown, excludes the possibility of the presence of protein granules, while the use of Fehling's test for sugar gives a decided reaction, if

strong cupric sulphate is used. Absolute alcohol does not cause the deposit of inulin crystals, and the absence of inorganic crystals is very noticeable. Imbedded in the protoplasm of the cells and scattered through it are granules which suggest starch, although the iodine test fails to show its presence in the fresh tubers. To be absolutely sure that these granules were not starch grains, I applied dilute sulphuric acid, washed off the acid with distilled water, and treated the sections with iodine. No reaction took place which would indicate the presence of starch. The presence of tannin, especially in the partially mature tubers, was revealed by the action of the juice on a bright razor blade. The bluish-black discoloration produced showed the formation of tannate of iron. This test is corroborated by a microchemic reaction in which the starch-like granules take part. Tannin vesicles have been observed in various phanerogams. These tannin vesicles always arise, as Klercker has shown, in the protoplasm, from which they are most probably separated by a true precipitation membrane of albumen tannate. Whether they contain other substances than tannins cannot at present be certainly stated. Especially useful in determining the presence of tannin is Pfeffer's staining *intra vitam* with methylene-blue. In a solution of this pigment, the cell sap which contains tannin and the tannin vesicles take up the blue color. This reagent applied to thick sections of *Nephrolepis* tubers produced a blue color in the starch-like granules (FIGURE 7) which had not reacted with the application of iodine, Bismarck brown, water-eosin, sulphuric acid and iodine, and acetic acid. That this test is decisive with reference to these granules is proved, I believe, by the presence of sugar in the older tubers, such sugar having been derived from the stored tannin. It is a known chemical fact that tannin may be converted into sugar by a complex reaction, and in all probability, although I have been unable to prove it, the tannin present in the living parenchyma-cells of the above fern species is slowly transformed into sugar which reacts in the older tubers to Fehling's solution.

The character of the reserve material stored in the tubers having been determined, it can be stated definitely that water storage is the principal function of them. The amount of water stored is very considerable. If a tuber is left in the sun to dry, it loses practi-

cally all of its weight and shrivels up to a small mass of dried material, only one twenty-fifth the size of the original tuber. The observations of Goebel\* are *apropos*. Goebel states that he found *Nephrolepis tuberosa* (perhaps *N. cordifolia*) as an epiphytic or terrestrial fern on the road to the Tankoban Prahoe volcano in Preanger, Java. He states that the tubers of this fern, the size of pigeon-eggs, are for the purpose of storing water, for he found that the water content was 96.3 per cent. of the total weight. He further proved this statement by placing tuber-bearing ferns in dry soil. The fronds remained green, although the water supply was extremely small. Gradually, however, the water disappeared from the tubers until they assumed a shrunken form. When grown in wet soil, the tubers retained their normal plumpness. The conclusion reached by Goebel, therefore, was that these tubers are of importance to the fern in tiding over shorter or longer periods of drought.

#### TUBERS OF ASPARAGUS SPRENGERI

This much-cultivated species of asparagus produces a considerable number of tuberous roots. The large secondary roots are about the thickness of a telegraph wire and on the lateral roots that grow from the larger ones occur the watery tubers† which range from twenty-five to forty-four millimeters in length and from eighteen millimeters in the larger tubers to ten millimeters in the smaller ones. They are light brown in color and almost perfectly smooth. From their distal extremity, the root is continued and this root continuation may branch and rebranch into numerous subsidiary branches.

Sections of these tubers mounted in water show large parenchyma-cells without solid contents, except in a few, small, scattered cells where bundles of raphides occur. With iodine the protoplasm which lines the cell-wall becomes yellow, and the complete absence of starch is also determined by this test. The large nuclei of these cells are also clearly shown when water-eosin is applied. These nuclei lie in the peripheral protoplasm and with the increase in size of the sap vacuole, the nucleus flattens out against the cell-wall in the thin layer of protoplasm remaining. Finally, the

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\* GOEBEL, K. Pflanzenbiologische Schilderungen I: 203.

† Strictly a tuber is a stem, or branch; I have used the word here in a lax sense.

nucleus disappears and the lining protoplasmic layer becomes still more contracted until it is difficult to detect. Absolute alcohol causes the contraction of the tubers, but no inulin is crystallized out by the use of this reagent. The application of Fehling's solution is without result, nor is tannin present, as the razor and methylene-blue tests indicate. Clearly, we are led to the conclusion that these tuberous roots are developed for the purpose of storing water and the necessity for the storage of this water is the same as in the fern species previously described.

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